

Original article

Responses of black willow (*Salix nigra*) cuttings to simulated herbivory and flooding

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Abstract

Herbivory and flooding influence plant species composition and diversity in many wetland ecosystems. Black willow (*Salix nigra*) naturally occurs in floodplains and riparian zones of the southeastern United States. Cuttings from this species are used as a bioengineering tool for streambank stabilization and habitat rehabilitation. The present study was conducted to evaluate the photosynthetic and growth responses of black willow to simulated herbivory and flooding. Potted cuttings were subjected to three levels of single-event herbivory: no herbivory (control), light herbivory, and heavy herbivory; and three levels of flooding conditions: no flooding (control), continuous flooding, and periodic flooding. Results indicated that elevated stomatal conductance partially contributed to the increased net photosynthesis noted under both levels of herbivory on day 30. However, chlorophyll content was not responsible for the observed compensatory photosynthesis. Cuttings subjected to heavy herbivory accumulated the lowest biomass even though they had the highest height growth by the conclusion of the experiment. In addition, a reduction in root/shoot ratio was noted for plants subjected to continuous flooding with no herbivory. However, continuously flooded, lightly clipped plants allocated more resources to roots than shoots. This study provides evidence that it is feasible to use black willow for habitat rehabilitation along highly eroded streambanks where both flooding and herbivory are present.

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1. Introduction

Herbivores can have demonstrable effect on plant populations. They affect plant fitness and population dynamics in several ways: (1) directly, through biomass removal, (2) indirectly, by altering competitive abilities in plant communities, and (3) indirectly, by altering the environment that the plant experiences (Mulder and Ruess, 1998; Begon et al., 1996). Much studies have been done to identify the influence of herbivory on plant functioning and performance such as biomass (Briggs, 1991), protein synthesis, plant growth regulator and secondary compounds (Hodkinson and Hughes, 1982; Edwards and Wratten, 1987), photosynthetic rates (Warrington et al., 1989; Peterson et al., 1996; Oleksyn et al., 1998), transpiration and nutrient uptake (Wallace and Macko, 1993), allocation of resources to shoots and roots, flowering, seed

production, seed survival, seedling and mature plant survival and vegetative growth (Gibson, 2002). However, the results of these studies are contradictory. A wide range of effects have been reported including reports of herbivores having no effect on their food plants, herbivores having negative impacts on their food plants, and herbivores enhancing plant growth and even plant fitness, i.e. overcompensation (Hjältén et al., 1993). It is also known that plant responses to herbivory vary, depending on prevailing abiotic and biotic conditions. However, the results of the ability of plant to compensate for lost tissues under different growth conditions are contradictory. Some workers have found that plants are more likely to overcompensate when water and nutrients are abundant (Belsky, 1987; Maschinski and Whitham, 1989), whereas others predicting that overcompensation tends to occur when plants are under stress (Oosterheld and McNaughton, 1991).

Black willow (*Salix nigra*) is the largest and the only commercially important willow among about 90 species native to North America. It is a flood-tolerant species that naturally

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occurs in floodplains and riparian zones of the southeastern United States (Mitsch and Gosselink, 1993). Black willow cuttings are extensively used as a cost-effective bioengineering tool to provide soil stabilization, erosion control, and habitat rehabilitation along highly eroded streambanks (Schaff et al., 2002). However, beavers (*Castor canadensis*) are commonly found in these areas. Beavers modify drainage network morphology and hydrology by cutting wood and building dams (Naiman et al., 1994). Willow (*Salix* sp.) is one of the woody plant preferences by beavers (Denney, 1952). The management of willow in grazed riparian ecosystems has received considerable attention (Meiman, 1995). Little Topashaw Creek (LTC), a fourth-order stream in the Yalobusha River watershed in north central Mississippi, has suffered accelerated channel erosion caused by poor watershed management practices and channelization. Black willow cuttings have been planted to restore eroded riparian streambanks (Martin et al., 2002). Our field observation revealed that most black willow cutting showed evidence of various densities of beaver herbivory.

In addition to herbivory effects, black willow cuttings are subjected to dynamic hydrologic conditions on streambanks. Depending on the slope and depth to base flow, plants may be exposed to continuous flooding or periodic flooding. Soil flooding initiates a chain of reactions leading to reduced soil conditions (low soil Eh) (DeLaune and Pezeshki, 1991). Reduced soil conditions may adversely affect plant physiological functioning such as plant nutrition, water relations, gas exchange and growth in many species (Pezeshki, 2001 and the references cited therein).

More studies have been conducted to investigate the responses of grasses or crops to herbivory than for woody plants. Meanwhile, little is known about the physiological responses (e.g. photosynthesis) in riparian ecosystems where plants are subjected to both reduced soil conditions and grazing. The purpose of this study was to examine the photosynthetic and growth responses of black willow cuttings to simulated herbivory and flooding. The research questions asked were: (1) Does flooding influence the response of black willow to simulated herbivory or vice versa? (2) Does simulated herbivory affect the photosynthesis and growth of black willow? If so, what are the underlying mechanisms? and (3) How does flooding affect the black willow functions?

2. Materials and methods

2.1. Plant materials

Black willow cuttings were collected from a small, localized population on the Loosahatchie River in western Tennessee, USA on May 24, 2002. Each cutting was ~0.65 cm in diameter at the base and 30 cm in length. All existing branches were removed from each cutting to conform to the common planting practices.

2.2. Experimental procedures

Cuttings were planted on May 26, 2002 in a greenhouse. Pots 20 cm high and 20 cm diameter were filled with two parts sand and one part silt (v/v). Holes were drilled on the side to allow control of soil moisture regime. One single cutting was planted in each pot with 1/3 of the cutting below ground and 2/3 above ground. The study was conducted in an air-conditioned greenhouse with an average daily low temperature of 27 °C and average daily high temperature of 40 °C. The only light source in the greenhouse from the natural light provided a daily photosynthetic photon flux density (PPFD) that ranged between 500 and 700 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at the top of the plant canopy during sunny days. Cuttings were fertilized with 50 ml of 20-20-20 Peters Fertilizer mixed with tap water at 1.25 g l^{-1} and applied to pots on June 12, June 20, July 8, July 16 and July 23. Plants were maintained well-watered and well-drained conditions prior to the treatments. The mean total biomass (root + shoot, excluding cutting) per plant was 4.55 g (± 0.45) and mean height was 49.3 cm (± 3.18) when the treatments were initiated on August 7, 2002. Plants grew under each treatment for 51 days after treatment initiation. Measurements of soil redox potential (Eh), plant photosynthetic and growth responses were made on days 8, 15, 30, 37 and 51.

Treatment consisted of three levels of flooding regimes: no flooding (control, well-watered and well-drained, NF), continuous flooding (flood water maintained at depth of 5 cm above the soil surface, CF), and periodic flooding (1 week of flood water maintained a depth of 5 cm above the soil surface followed by a week of well-watered and well-drained condition, PF). In addition, three levels of simulated herbivory were imposed: no herbivory (control, unclipped, NH), light herbivory (1/3 of the height was clipped, LH), and heavy herbivory (2/3 of the height was clipped, HH). Ten potted cuttings were assigned randomly to each of nine treatment combinations for a total of 90 pots.

2.3. Soil measurements

Six platinum-tipped electrodes were inserted in soil at depth of 10 cm per flooding treatment (one electrode per pot). Soil redox potential (Eh) was monitored using a Model 250A ORION millivolt redox meter and a calomel reference electrode (Thermo Orion, Beverly, MA, USA) on each sampling day. An Eh value of +350 mV represents the approximate level at which oxygen begins to disappear from the soil (DeLaune and Pezeshki, 1991). Soil Eh for control (NF) remained above +400 mV for the duration of the experiment indicating oxic condition in well-drained treatment. Soil was reduced in CF after 1 week of treatment and the level of soil Eh was remained in mildly reduced range (+322 to +195 mV). In PF, Eh cycled between mildly reduced and oxic conditions in response to flooding and draining periods (Fig. 1).

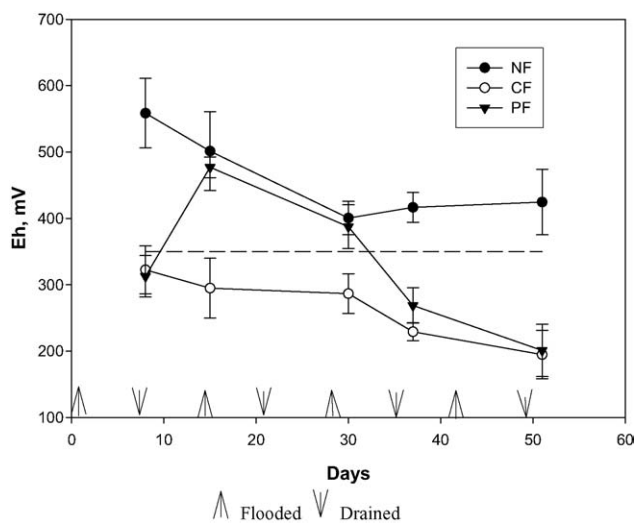


Fig. 1. Soil redox potential (Eh) recorded for no flooding (NF), continuous flooding (CF) and periodic flooding (PF) treatments. The dashed line at +350 mV represents the approximate level at which oxygen begins to disappear from the soil (DeLaune and Pezeshki, 1991). Each value is the mean for six replications \pm 1 S.E. The arrows symbolize the initiation of flooding and draining for PF treatment.

2.4. Photosynthetic responses

Measurements of net photosynthesis (P_n , $\mu\text{mol m}^{-2} \text{s}^{-1}$) and stomatal conductance (g_w , $\text{mmol m}^{-2} \text{s}^{-1}$) were conducted using a portable gas exchange analyzer (Model CIRAS 1, PP Systems, Havertown, MA, USA). On each sampling day between the hours of 08:00 and 12:00, five cuttings from each treatment were randomly chosen and the third or fourth well-developed leaf of the tallest shoot was used to conduct the measurements (one measurement per plant). Immediately after these measurements, leaf chlorophyll content (cci units, the correspondence between cci units and chlorophyll content (mg g^{-1}) $R^2 = 0.72$) was recorded on the same leaves using a Model CCM-200 chlorophyll content meter (OptiSciences, Tyngsboro, MA, USA).

2.5. Height growth and biomass

The height (cm) was measured immediately after the initiation of the treatment and at the conclusion of the experiment for all study plants. Height growth was calculated as the difference between the final height and initial height. Total biomass production (i.e. shoot + root, g) and biomass allocation (i.e. root/shoot ratio) excluding the biomass removed by simulated herbivory were recorded only at the end of the experiment because it required destructive sampling. Each plant was divided into shoot and root components. Plant components were then dried at 70 °C to a constant weight and dry weights were recorded. Root/shoot ratio was calculated as the ratio of dry root weight to dry shoot weight.

2.6. Data analyses

The experiment followed a completely randomized design. Three-way MANOVA (SPSS 11.5) with three levels of flood-

ing, three levels of simulated herbivory and five levels of sampling date was used to test the differences in means for photosynthetic responses including net photosynthesis, stomatal conductance and chlorophyll content. Two-way ANOVA (SPSS 11.5) with flooding and simulated herbivory was used to test the differences in means of height growth and biomass. The Tukey procedure was used to examine all pair-wise group differences. Differences were considered significant at $P < 0.05$.

3. Results

3.1. Photosynthetic responses

There was no significant interaction among flooding, simulated herbivory and sampling date, between flooding and herbivory or between flooding and sampling date, but significant interaction between herbivory and sampling date was noted. Since flooding treatment was not involved in any significant interaction, the main effect of flooding on photosynthetic function was tested, and it was not significant (Table 1). Simple main effects analysis was conducted for the interaction of herbivory and sampling date. Photosynthetic responses showed differences between three herbivory treatment groups on all five sampling days (day 8: $F_{(6, 80)} = 3.949$, $P = 0.002$; day 15: $F_{(6, 52)} = 3.196$, $P = 0.010$; day 30: $F_{(6, 70)} = 5.455$, $P < 0.001$; day 37: $F_{(6, 80)} = 3.118$, $P = 0.009$ and day 51: $F_{(6, 76)} = 2.594$, $P = 0.024$) after one-way MANOVA was conducted. The results of the pair-wise comparisons between each pair of herbivory treatments on each sampling day indicated that net photosynthesis was enhanced in both LH and HH groups on day 30 when compared to NH group. Stomatal conductance was significantly higher for heavily clipped plants on all sampling days except day 51. The LH treatment group exhibited greater stomatal conductance than NH group on all dates except 8 and 37. There were no significant differences noted between HH and LH. In addition, leaf chlorophyll content was stimulated in the LH treatment compared to NH on day 8. On days 8 and 37, it was higher in LH plants than HH (Fig. 2 and Table 2).

3.2. Height growth and biomass

Simulated herbivory and flooding had no additive effect on height growth and total biomass production. Again, flood-

Table 1

MANOVA table (F value, df and P value) for the simple effects and interactions for net photosynthesis, stomatal conductance and chlorophyll content on black willow cuttings in response to flooding and simulated herbivory on five sampling days

Effect	F	df	P
Flooding \times herbivory	1.675	12, 415.67	0.070
Flooding \times day	1.065	24, 455.95	0.381
Herbivory \times day	1.640	24, 455.95	0.030
Flooding \times herbivory \times day	1.303	48, 467.75	0.091
Herbivory	11.740	6, 314.00	<0.001
Day	8.340	12, 415.67	<0.001
Flooding	0.380	6, 314.00	0.683

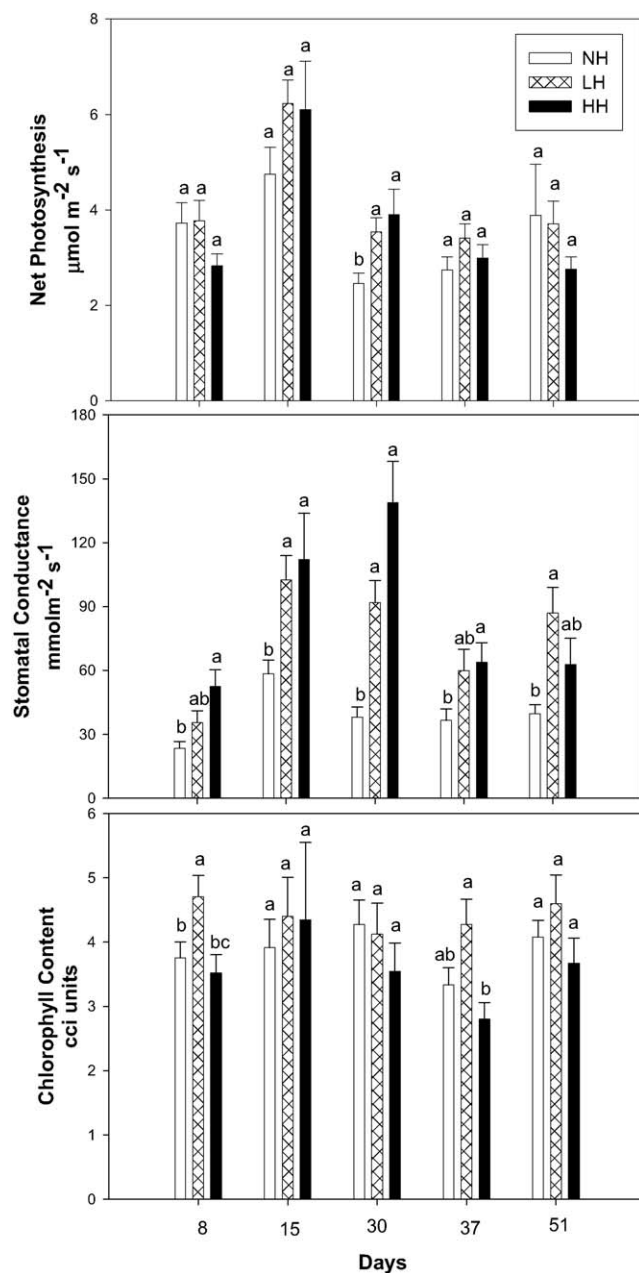


Fig. 2. Net photosynthesis (P_n , $\mu\text{mol m}^{-2} \text{s}^{-1}$), stomatal conductance (g_w , $\text{mmol m}^{-2} \text{s}^{-1}$), and chlorophyll content (cc units) for black willow cuttings in three simulated herbivory treatments (no herbivory, NH; light herbivory, LH; heavy herbivory, HH) across all flooding conditions on each sampling day. Significant differences are shown across herbivory treatments using different letters. Each value is the mean for 15 replications \pm 1 S.E.

ing had no significant effect on these two growth measurements. But differences existed between the three levels of herbivory. Height growth was 282.5% higher in HH group than in NH (Fig. 3 and Table 3). However, total biomass that the HH group accumulated was only 53.4% of NH at the conclusion of the experiment (Fig. 4). There were no significant differences in height growth or biomass accumulation between LH and NH groups (Figs. 3 and 4).

There was an interaction between simulated herbivory and flooding for root/shoot ratio (Table 3). A reduction in

root/shoot ratio was noted under CF as compared to the NF when NH treatment was applied. Under LH condition, CF plants responded with higher root/shoot ratio than PF plants (Fig. 5). Roots and shoots responded to three herbivory conditions under both NF and PF treatments in a similar manner (Fig. 7), thus having no differences in root/shoot ratio (Fig. 6). However, when the soil was continuously flooded, both light and heavy herbivory treatment groups showed higher root/shoot ratio than controls (Fig. 6). High root/shoot ratio in HH plants was due to shoot biomass reduction by simulated herbivory (Fig. 7). While under LH condition, high root/shoot ratio resulted from shoot biomass removal and more resource allocation to roots than shoots (Fig. 7).

4. Discussion

In the present study, photosynthetic rates were significantly increased in plants under both simulated herbivory treatments on day 30 (Fig. 2). Overcompensation has long been considered to be an adaptive response that evolved as a consequence of natural selection due to herbivory (Crawley, 1987). A greater photosynthetic rate of leaves on defoliated plants than for comparable age leaves on undefoliated plants is defined as compensatory photosynthesis (Nowak and Caldwell, 1984).

Although compensatory photosynthesis has been observed in many plant species (Wallace, 1990; Atkinson, 1986), much less is known about the response mechanisms involved. For example, ribulose-1, 5-bisphosphate carboxylase/oxygenase (rubisco) activity or amount, chlorophyll content and leaf conductance have been implicated compensatory photosynthesis (Yamashita and Fujino, 1986; Nowak and Caldwell, 1984; Heichel and Turner, 1983). Our results indicated that among other factors, the enhanced stomatal conductance of clipped plants on day 30 (Fig. 2) contributed to the compensatory photosynthesis. However, leaf chlorophyll content was not responsible for the increased photosynthesis (Fig. 2). In addition, net photosynthesis was increased slightly under both herbivory treatments as compared to control on days 15 and 37 even though the differences were not significant at $P < 0.05$ (Fig. 2). However, towards the end of the experiment, there was no photosynthetic stimulation due to herbivory treatments. The reason may be that black willow cuttings had acclimated to the shoot biomass removal.

Studies have demonstrated that herbivory intensity is an important factor governing plant responses and performance (Reich et al., 1993; Ellsworth et al., 1994). For example, severely treated boreal willow (*Salix myrsinifolia-phylicifolia*) showed a large increase in shoot numbers, while less damaged plants produced fewer shoots (Elmqvist et al., 1987). Even though we did not find significant differences in photosynthetic rates between LH and HH plants (Table 2 and Fig. 2), the height growth and biomass production responded to HH and LH treatments differently across flooding treatments. The HH plants compensated for the lost shoot biomass with

Table 2

Pair-wise comparison (F value, df and P value) between simulated herbivory treatments (no herbivory, NH; light herbivory, LH and heavy herbivory, HH) for net photosynthesis (P_n), stomatal conductance (g_w) and chlorophyll content for black willow cuttings across all flooding conditions on each sampling day

Day	Pair	Multivariate tests			Univariate tests						
		F	df	P	df	P_n		g_w		Chlorophyll content	
						F	P	F	P	F	P
8	NH–LH	3.777	3, 26	0.023	1, 28	0.006	0.939	3.443	0.075	5.324	0.029
	NH–HH	5.633	3, 26	0.004	1, 28	3.356	0.078	12.110	0.002	0.385	0.540
	LH–HH	4.411	3, 26	0.012	1, 28	3.642	0.067	3.174	0.086	7.488	0.011
15	NH–LH	6.789	3, 23	0.002	1, 25	3.861	0.061	11.679	0.002	0.428	0.519
	NH–HH	4.888	3, 14	0.016	1, 16	1.295	0.272	10.737	0.005	0.180	0.677
	LH–HH	0.047	3, 13	0.986							
30	NH–LH	7.925	3, 24	0.001	1, 26	8.846	0.006	24.095	<0.001	0.062	0.086
	NH–HH	3.696	3, 23	<0.001	1, 25	7.198	0.013	31.065	<0.001	1.574	0.221
	LH–HH	1.979	3, 21	0.148							
37	NH–LH	1.766	3, 26	0.178							
	NH–HH	3.514	3, 26	0.029	1, 28	0.420	0.522	6.609	0.016	2.059	0.162
	LH–HH	3.622	3, 26	0.026	1, 28	1.080	0.307	0.081	0.778	9.886	0.004
51	NH–LH	6.438	3, 24	0.002	1, 26	0.023	0.879	13.470	0.001	1.034	0.319
	NH–HH	1.725	3, 25	0.187							
	LH–HH	2.403	3, 25	0.091							

increased height growth (Fig. 3), which was the result of enhanced photosynthetic rate on most of the measurement days since the process of photosynthesis provides the energy (carbohydrate) for plant growth and maintenance. But the average plant final height at the end of the experiment was the shortest in the HH group (data not shown) and the biomass production of this group was also lower than that in the

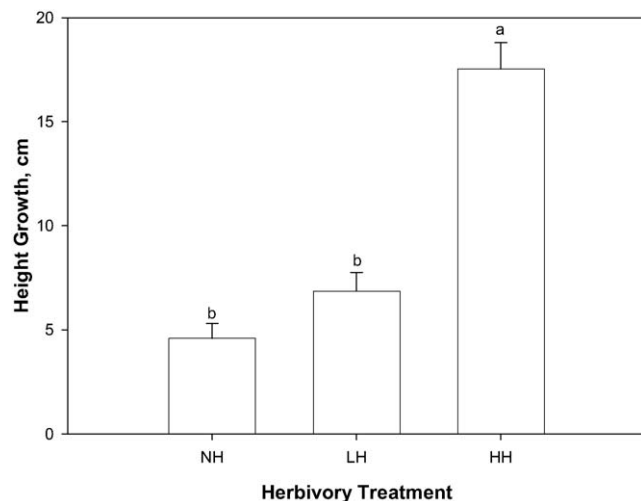


Fig. 3. Height growth for black willow cuttings in three simulated herbivory treatments across all flooding conditions: no herbivory (NH), light herbivory (LH) and heavy herbivory (HH). Significant differences are shown across treatments using different letters. Each value is the mean for 30 replications ± 1 S.E.

Table 3

ANOVA table (F value, df and P value) for the simple effects and interactions for height growth, total biomass and root/shoot ratio on black willow cuttings in response to flooding and simulated herbivory

Source of variation	df	Height growth		Total biomass		Root/shoot ratio	
		F	P	F	P	F	P
Flooding	2	0.578	0.564	1.386	0.262	6.10	0.005
Herbivory	2	38.72	<0.001	23.812	<0.001	3.96	0.028
Flooding \times herbivory	4	0.75	0.560	1.19	0.332	2.90	0.036

other two groups (Fig. 4), suggesting that the HH plants did not recover from the heavy herbivory effects for the duration of our experiment. The reasons for this might be that woody plants, including willow, have a lower ability to regenerate lost tissue compared with short-lived, fast growing grasses and herbs (Maschinski and Whitham, 1989). It has also been reported that the capability to recover from herbivory depends on when it occurs during the season (Maschinski and Whitham, 1989). In this study the simulated herbivore event occurred in the middle of the growing season, and the time left for recovery was limited. Thus, a longer experimental period might have allowed the HH plants to accumulate greater amounts of biomass by the conclusion of the experiment. In contrast, the height growth and the final total biomass of LH plants were not significantly different from NH plants, which indicated that light herbivory did not affect the growth of black willow as heavy herbivory did. This result confirmed that in studies of plant responses to herbivory, the intensity of damage is of critical importance.

Besides the timing and intensity of the herbivory, frequency is also very crucial (Jameson, 1963). Abbott et al. (1993) concluded that more frequent defoliations of low intensity reduce growth of Jarrah (*Eucalyptus marginata*) more than less frequent defoliation of higher intensity. In the field, beavers may cut the black willow cuttings once or more over the course of the growing season. However, the present study only addressed a one-time simulated herbivory effect. The effect

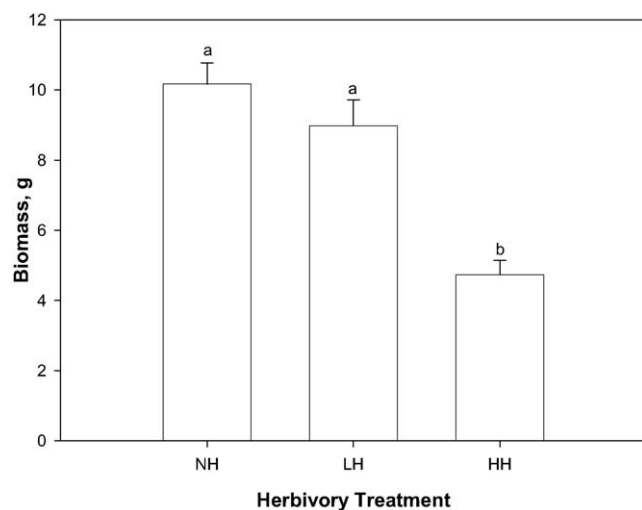


Fig. 4. Biomass production for black willow cuttings in three simulated herbivory treatments across all flooding conditions: no herbivory (NH), light herbivory (LH) and heavy herbivory (HH). Significant differences are shown across treatments using different letters. Each value is the mean for 30 replications \pm 1 S.E.

of frequent herbivory on this species needs additional investigation.

As far as the flooding effects on this species, our data did not show any significant differences in photosynthetic responses, height growth and biomass production among the three soil moisture treatment groups. However, many studies have suggested that decrease in photosynthetic rates and growth is a common plant response to low soil Eh conditions (Pezeshki, 2001 and the references cited therein). For example, a decrease in soil Eh from +540 to -225 mV reduced net photosynthesis in nuttall oak (*Quercus nuttallii*) and bald-cypress (*Taxodium distichum*) by 76% and 19%, respectively (Pezeshki and Anderson, 1997). Photosynthesis, root growth

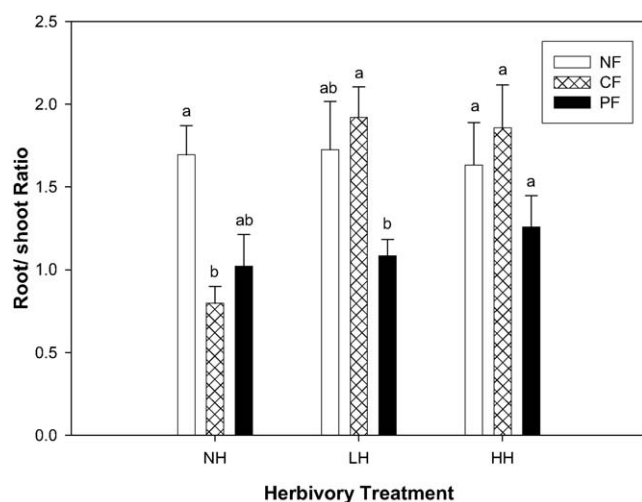


Fig. 5. Root/shoot ratio for black willow cuttings in three flooding treatments (no flooding, NF; continuous flooding, CF; periodic flooding, PF) under three simulated herbivory conditions (no herbivory, NH; light herbivory, LH; heavy herbivory, HH). Significant differences are shown across flooding treatments under the same herbivory condition using different letters. Each value is the mean for 10 replications \pm 1 S.E.

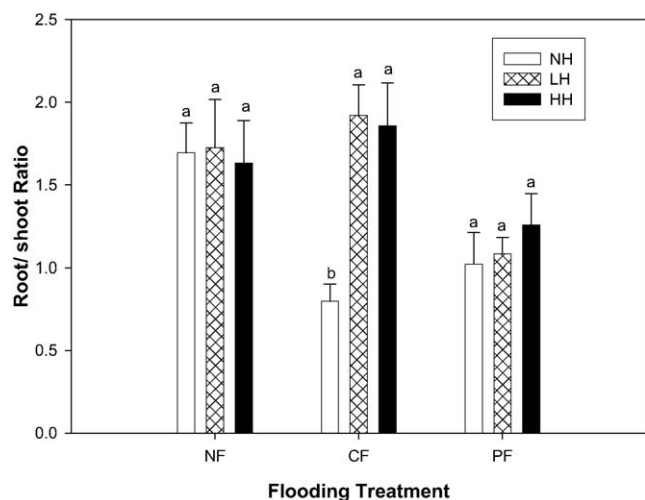


Fig. 6. Root/shoot ratio for black willow cuttings in three simulated herbivory treatments (no herbivory, NH; light herbivory, LH; heavy herbivory, HH) under three flooding conditions (no flooding, NF; continuous flooding, CF; periodic flooding, PF). Significant differences are shown across herbivory treatments under the same flooding condition using different letters. Each value is the mean for 10 replications \pm 1 S.E.

and biomass in rice (*Oryza sativa*) were inhibited under low soil Eh conditions (Kludze and DeLaune, 1995). Our results indicated that black willow is rather tolerant to flooding as was demonstrated by its ability to withstand the mildly reduced soil conditions at the physiological levels. This finding is in agreement with the previous studies of responses of black willow to moderately reducing soil conditions (Pezeshki et al., 1998; Schaff et al., 2003). The highly reduced soil redox condition has been reported to lead to decreased gas exchange in this plant species (Pezeshki et al., 1998).

The present study demonstrated a significant interaction between flooding and simulated herbivory with respect to root/shoot ratio. When heavy herbivory was applied, both root and shoot biomass responded to NF, CF and PF in a similar manner, thus having no differences in root/shoot ratio (Fig. 5). The CF plants allocated more resources to shoot than root as compared to the NF when no herbivory was applied thus, having the low root/shoot ratio (Fig. 5). It has been confirmed that plant root was more sensitive to reducing soil conditions than shoot in many species (Kludze and DeLaune, 1994; Pezeshki, 1991). However, when 1/3 of the height was clipped (LH), CF cuttings tended to accumulate more root biomass than shoot biomass relative to those subjected to PF (Fig. 5). Soil condition in PF condition shifted from anoxic to oxic because of flooding and draining. Therefore, the plants had the opportunity to recover root growth during the drained periods. It has been reported that the aboveground herbivory may lead to an increase in the root/shoot ratio due to removal of aboveground structures and the stimulation of root growth (Gibson, 2002). It seemed that black willow cuttings were more sensitive to light herbivory than continuous flooding with respect to the biomass partitioning. The results suggested that the root growth of wetland plants is inhibited by flooding. However, when beavers are present, a low level of grazing could stimulate root growth.

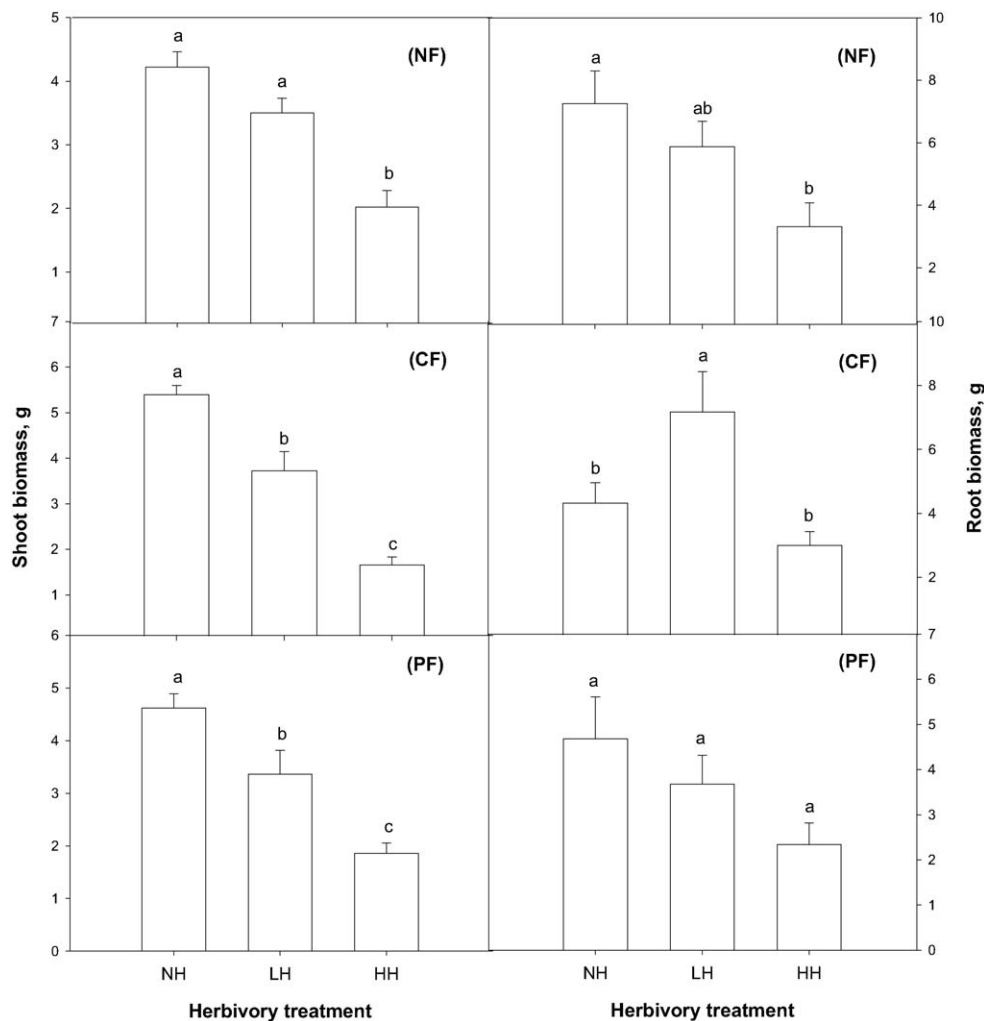


Fig. 7. Shoot and root biomass for black willow cuttings in three simulated herbivory treatments (no herbivory, NH; light herbivory, LH; heavy herbivory, HH) under three flooding conditions (no flooding, NF; continuous flooding, CF; periodic flooding, PF). Significant differences are shown across herbivory treatments under the same flooding condition using different letters. Each value is the mean for 10 replications \pm 1 S.E.

Another interesting finding of this study was that roots and shoots responded to the simulated herbivory levels under both NF and PF treatments in a similar manner (Fig. 7), maintaining a relatively constant root/shoot ratio (Fig. 6). In contrast, under CF condition, plants in both herbivory treatments had higher root/shoot ratio than controls (Fig. 6). High root/shoot ratio in HH plants was due to less shoot biomass after the simulated herbivory (Fig. 7). Conversely, under LH condition, the results again suggested that CF plants allocated more resources to root growth than to shoots (Fig. 7).

Previous research has indicated extreme soil moisture governs the survival and functioning of black willow cuttings planted to restore riparian zones along degraded stream corridors (Schaff et al., 2003; Schaff et al., 2000; Pezeshki et al., 1998). Herbivory, however, is another factor that plays an important role in the success of the rehabilitation project. Our results provide evidence that black willow is well adapted to a reduced soil environment, albeit at the moderate levels of reduction tested in this study, and can survive at stream restoration sites where both extensive, infrequent herbivory and flooding are common occurrences.

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